

A lion found in the Egyptian tomb of Maïa

Burial of a mummified lion at a dedicated site confirms this animal's once-sacred status.

Lions are mentioned by classical scholars and in pharaonic inscriptions as being among the sacred animals that were bred and buried in the Nile valley. And yet no specimens have been found in Egypt — until the excavation of the Bubasteion necropolis at Saqqara. Here we describe a complete skeleton, once a mummy, of a male lion (*Panthera leo*) that was discovered there, buried among the cats' catacombs¹ created during the last centuries BC and occupying the much older tomb of Maïa, wet-nurse to the king Tutankhamun (from the New Kingdom, fourteenth century BC). This important find at a site that was dedicated to the feline goddess Bastet (also known as Bubastis) confirms the status of the lion as a sacred animal during the Late and Greek periods.

Rock-cut tombs of the XVIIIth and XIXth dynasties have been excavated by the French Archaeological Mission of the Bubasteion (MAFB) on the site of Saqqara, cemetery of Memphis. These New Kingdom tombs have been partly reused as cats' catacombs and are located inside the Bubasteion precinct dedicated to the cat (once lioness) goddess Bastet during the last centuries BC (see supplementary information).

The tomb of Maïa (Fig. 1) was discovered by MAFB in 1996. It includes at least two levels: the chapel and the funerary apartments. The funerary apartments have no remains of the original burial and have been reoccupied by intrusive burials, first of humans and then of animals (mainly cats). The main funerary level is divided into three rooms connected by corridors. Room number one is roughly L-shaped and is supported by a rock-cut pillar, whereas room number two is smaller and roughly rectangular in shape, with a shaft leading to a lower and less important level. Room number three (4.5 m by 4 m) has been carefully hewn and prepared. The floors of these three rooms were covered with wooden coffins or sarcophagi and many decayed human and animal remains, with huge quantities of bones. The most numerous occupants were mummified cats, but stratigraphic features prove that the humans were deposited there beforehand, perhaps several centuries earlier.

While working in the main room of the funerary level in November 2001, we made the surprising discovery of a virtually complete, undisturbed skeleton



Figure 1 Sacred burial of a lion (*Panthera leo*). Left, King Tutankhamun and his wet-nurse, lady Maïa, on a relief carved in the chapel of her tomb. Right, skeleton of the once-mummified lion lying on the floor of room 3 in the funerary level of the tomb.

of a felid that was much larger than the cats found previously. It was a lion, lying on a rock (Fig. 1) with its head turned northwards and its body orientated to the east. The lion was surrounded by numerous animal bones and coffins that were partly destroyed and buried much later than the human occupant (see supplementary information).

The conservation of this *Panthera leo* specimen was excellent, except that the skull was partly crushed and the scapula and

femur had been damaged. Although there were no linen bandages to indicate that the body had been mummified, there is other evidence to indicate that it had — namely, the position of the skeleton, the presence of small and degraded fragments of tissue inside the cavity of the canine teeth, and deposits on and coloration of the bones that are similar to those of mummified cats discovered on the site.

At first sight, the general position of the



Figure 2 Skeletal features of the lion lying in Maïa's tomb. A scale drawing is shown of the skeleton of the *Panthera leo* specimen: blue, forelimbs (dark, right side; light, left side); yellow, hindlimbs (dark, right side; light, left side). Drawing courtesy of C. Callou/MAFB. © Hypogées. Inset, lower mandible of the *Panthera leo* found at Saqqara. Regrettably, it is impossible to give a precise age for the skeleton because of the poor dental state. The most remarkable dental abnormality is observed on the superior and lower canines. Their occlusal surfaces are perfectly smooth and very worn. Moreover, the dental crown is extremely low, ground down to just above the neck. Premolars and molars, upper and lower, are also markedly altered. It seems that this change results from extreme wear, because only the basal parts of roots of all the teeth remain. Only the chewing of very tough materials (such as pebbles) can explain such modifications of the teeth. Moreover, the aspect of the jaw is due to important and continuous pathologies, doubtless connected to deficiencies. This project was carried out with the permission of the Supreme Council of Egyptian Antiquities, Cairo. Photo, P. Chapuis/MAFB. © Hypogées.



skeleton is reminiscent of the position of the mummies of cats, even though the disposal of the hindlimbs is different. In the case of the lion, the forelimbs and the hindlimbs are stretched down along the front of the body, with the tail returned between the paws, but in the cats' mummies, the hindlimbs were tucked up against the pelvis with the tail curled up between the feet (Fig. 2). The bones are in strict connection, except the calvarium, which had fallen slightly behind, probably when the packaging disintegrated.

As the bone measurements are among the largest recorded for a male lion and outside the range of variation shown by females (C. Gross, personal communication), there is no doubt that this skeleton is from a male lion (see supplementary information). In contrast to results revealed by X-rays of many cat mummies^{1,2}, there is no indication that the animal was killed when young in order to be mummified and buried. It is likely that it died naturally.

Complete epiphyseal fusion of the skeleton and the very weak pulp chamber of the teeth show that they belong to an adult. The wear and pathology of the teeth (Fig. 2) suggest that the lion lived to be old and was kept in captivity. Seven ribs, on the same side of the chest, are fractured in the middle and have calluses formed on them; they may have broken as a result of a fall or a violent knock.

The existence of lions during the time of the pharaohs has been frequently described³, but to our knowledge this is the first complete skeleton to be found in Egypt (though some bones were found in Abydos⁴). The discovery should convey valuable information about the animal and its life (age, pathologies and accidents). Although buried in the tomb of a woman from the XVIIIth dynasty (about 1430 BC), the animal belongs to the later Bubasteion catacombs connected to the cult of animals that was so important in Late and Hellenistic Egypt (see supplementary information).

As a male, the mummified lion may have been considered as an incarnation of the god Mahes (Mysis)⁵, son of the goddess Sekhmet or Bastet. Although a single lion burial does not constitute a lion necropolis, this Memphite specimen confirms the existence of lions in Egypt in the last centuries BC. Lions are thought to have been bred in sanctuary precincts and buried in a sacred animal necropolis, including the Memphite necropolis (as suggested by demotic and Greek inscriptions⁶ and by some claws with evidence of mummification⁷).

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Olfaction

Mosquito receptor for human-sweat odorant

Female *Anopheles* mosquitoes, the world's most important vector of *Plasmodium falciparum* malaria, locate their human hosts primarily through olfactory cues¹, but the molecular mechanisms that underlie this recognition are a mystery. Here we show that the *Anopheles gambiae* protein AgOr1, a female-specific member of a family of putative odorant receptors^{2,3}, responds to a component of human sweat. Compounds designed to activate or block receptors of this type could function as attractants for trapping mosquitoes or as insect repellents in helping to control *Anopheles* and other insect pests.

A member of the AgOr gene family, AgOr1, was expressed in an engineered neuron of the fruitfly *Drosophila*. The neuron failed to respond normally to odours because its endogenous odorant-receptor genes, *Or22a* and *Or22b*, had been deleted. AgOr1 was expressed in this mutant by using an *Or22a* promoter and the *GAL4-UAS* system⁴. We assayed the response of this neuron to individual odours by single-unit electrophysiology.

We found that AgOr1 confers a strong response to the odorant 4-methylphenol (Fig. 1a). As this compound is a component of human sweat that elicits an electrophysiological response from the antenna of female *A. gambiae*⁵, it may contribute to the anthropophilic host-seeking behaviour of this mosquito. This idea is supported by the fact that AgOr1 is expressed specifically in the olfactory tissue of only female mosquitoes, and its expression is downregulated after a blood meal² (the host-seeking behaviour of these mosquitoes is specific to the female and is reduced after blood-feeding⁶). Furthermore, 4-methylphenol increases the effectiveness of traps for the tsetse fly *Glossina morsitans morsitans*⁷.

We tested a second AgOr gene, AgOr2, and found a different odour-response spectrum (Fig. 1b). In contrast to AgOr1, AgOr2 confers a strong response to 2-methylphenol

but not to 4-methylphenol. There was no response in the case of the deletion mutant carrying no transgene (Fig. 1c).

These results indicate that this pair of AgOr genes encodes odorant receptors, and that the female-specific receptor AgOr1 may participate in the host-seeking behaviour of *A. gambiae*. As mosquito odorant receptors can function in *Drosophila* in the absence of other mosquito proteins, there could be a compatibility between odorant receptors and olfactory-receptor neurons from different species, which would allow the fruitfly to be used as an *in vivo* model for the study of odorant receptors derived from less genetically tractable insect species.

Anopheles mosquitoes transmit malaria and are responsible for the death of more than one million people each year. Our discovery that this mosquito possesses odorant receptors for particular components of human sweat means that different ligands could be screened for their activation or inhibition of these receptors, potentially

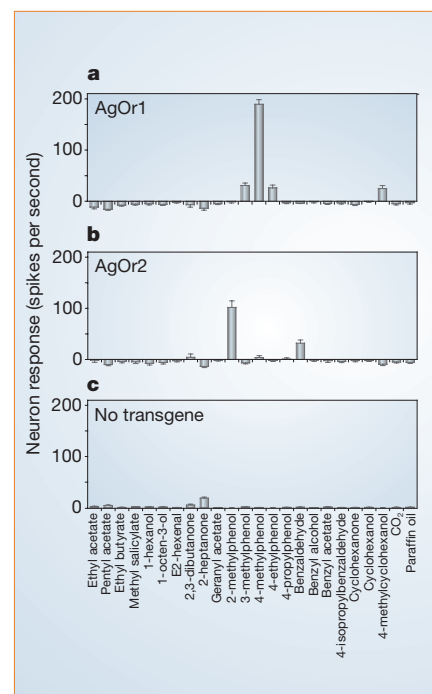


Figure 1 Identification of a mosquito odorant receptor that responds to a component of human sweat by expression in a *Drosophila* olfactory receptor neuron. **a–c**, Odour-response spectrum conferred by AgOr1 (**a**) and AgOr2 (**b**) on a *Drosophila* olfactory neuron carrying a deletion of its endogenous receptor genes (response of deletion mutant without transgenes is shown in **c**). Transgenic flies were of the genotype *w¹¹¹⁸; Δhalo/Δhalo*; *UAS-AgOr/Or22a promoter-Gal4* (refs 4,8). Single-unit recordings were obtained⁴ from animals that were less than one week old. Liquid odour sources were diluted by 10^{−4} in paraffin oil; solid odour sources were diluted to 0.2 mg ml^{−1} in paraffin oil; CO₂ was administered as described in ref. 4. Responses were quantified by subtracting the number of spikes in 500 ms of spontaneous activity from the number in the 500 ms after the onset of odour stimulation (*n* = 12; error bars represent s.e.m.). AgOr cDNA clones were from *Anopheles gambiae sensu stricto* (G3 strain); embryos (provided by M. Benedict) were reared as described⁸.